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The Symptoms of Spindle Tuber and Unmottled Curly Dwarf of the Potato

R. W. GOSS
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Lincoln, Nebraska
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SUMMARY

1. A study has been made of the symptoms of spindle tuber and unmottled curly dwarf in the Bliss Triumph variety and of the environmental modification of the symptoms.

2. A brief review of the descriptive literature is presented and the identity of the two diseases as determined by inoculation experiments is discussed.

3. The occurrence of unmottled curly dwarf in commercial fields and the possibility of its having been present for some years are noted.

4. A modification of symptoms occurs when plants are grown under glass and this varies with the length of the rest period of the seed tubers. With a short rest period the vine symptoms are very slight and the two diseases are almost indistinguishable, while with later plantings the symptoms of unmottled curly dwarf are similar to those occurring in the field.

5. The tuber symptoms of both diseases were found to be increased in severity with an increasingly high soil moisture content. The vine symptoms of spindle tuber were obscured by the luxuriant growth with high moisture but the reverse condition occurred with the tubers, the symptoms being most severe at high moistures. The same general effect occurred with unmottled curly dwarf but the symptoms of both vines and tubers were more severe than with spindle tuber grown at the same moisture content.

6. Healthy tubers produced at a high soil moisture content appeared more like spindle tuber than the infected tubers produced at a low soil moisture content.

7. High soil temperatures were found to have the same effect as high soil moisture in regard to tuber symptoms with both diseases and with the healthy checks. With high soil temperatures the vine symptoms were also more severe.

8. The development of sprout tubers by unmottled-curly-dwarf seed and the lack of apical dominance with both diseases were noted. The variability of these abnormalities makes them of little value for diagnostic purposes.

9. The effect upon the symptoms of seed treatments designed to break the rest period was studied. Such treatments hastened sprouting and thus obscured the retardative symptom but neither the vine nor the tuber symptoms were modified.

10. Spindle-tuber and unmottled-curly-dwarf tubers have a low respiration rate as indicated by the effect of holding in closed containers. Under conditions detrimental to healthy tubers the rest period of infected tubers was shortened and sprout development was stimulated.

11. Attempts to identify the diseases by chemical tests were largely negative. Infected tubers of both diseases showed a larger content of nitrates than healthy tubers by qualitative tests, but the variability was too great to make the test of practical value.

12. The differential values of the various symptoms of spindle tuber and unmottled curly dwarf as regards both the vine and tuber symptoms are tabulated and discussed.

13. The modification of symptoms by environmental factors was great enough to make it impossible to distinguish accurately between

spindle tuber and unmottled curly dwarf or between healthy and infected vines and tubers when produced under dissimilar conditions. The plant character as a whole rather than any individual symptom must be relied upon to differentiate the diseases, as unmottled curly dwarf vines are distinguished from spindle tuber chiefly by a more severe manifestation of similar symptoms. The same thing was true of the tuber symptoms, any one symptom being insufficient to identify the diseases accurately. The eye characters were found to be the most constant symptoms and were less subject to environmental effects than the tuber shape. While of great value in separating healthy from infected tubers, the eye characters alone were insufficient to separate the two diseases.

The Symptoms of Spindle Tuber and Unmottled Curly Dwarf of the Potato

R. W. GOSS

The differentiation of the virus diseases of the potato on the basis of symptoms is an important but difficult phase of the virus problem. A knowledge of the variation in symptoms due to environmental factors is necessary both in investigational work and in the practical application of our knowledge to the control of these diseases in the field. A fairly comprehensive knowledge of the masking effect of certain environmental factors upon the symptoms of the mosaic group has been obtained thru the work of various investigators. Considerably less information is available concerning the effect of environment upon the symptoms of spindle tuber and practically no information is available regarding unmottled curly dwarf.

The author (4) and the author with Peltier (6) have previously reported the effect of certain environmental factors upon the symptoms of spindle tuber. During the progress of those investigations, however, Schultz and Folsom (15) described a new virus disease and named it "unmottled curly dwarf." The symptoms described for this disease correspond very closely to certain manifestations of the spindle-tuber disease, referred to by various workers as "severe spindle tuber." It was thought that the previous work had possibly included both diseases and it was therefore considered desirable to repeat the work in more detail with spindle tuber and to compare, under various environmental conditions, the symptoms of spindle tuber with those of the newly described disease, unmottled curly dwarf. The present paper reports the results of these investigations, which were conducted entirely with the Bliss Triumph variety.

REVIEW OF LITERATURE[1]

Spindle tuber.—Schultz and Folsom (15) and Folsom (2) describe the symptoms of spindling-tuber (spindle tuber) as being characterized by erect, spindling stalks, with dwarfed, rugose leaves, more erect and of darker green than normal leaves. The tubers are described, in comparison with the normal, as being more cylindrical, more spindling, and with a more irregular or bumpy outline; the eyes as being more numerous and more conspicuous and the skin as smoother and

[1] The terms used in describing symptoms in this publication are those defined by Schultz and Folsom (15, p. 44).

more tender; the color of the skin as changing to a browner and duller color with Irish Cobblers and a lighter pink and blotchy color with Bliss Triumphs.

Other investigators have published quite similar descriptions and only those that add to the description given above will be considered. Fernow (1) mentions a marginal rolling of the leaves. Martin (8) in the first published account of the disease under the name spindle tuber also mentions marginal leaf rolling and the additional symptom of growth cracks in the tubers. MacLeod (7) notes that "The midribs of lateral leaflets occurring at the top of seriously affected plants are sometimes inwardly curved so that these leaflets tend to overlap each other and the terminal leaflet as well, giving the plant what is popularly called a 'bow-legged' appearance." He states that the main petiole is often more slender and may become slightly brittle. In regard to tuber symptoms he mentions one additional characteristic, that of protruding brows associated with the shallow, conspicuous eyes.

Werner and Howard (13) describe in considerable detail the "running out" of potato seed stocks with which they worked in Nebraska and they conclude that this was identical with spindle tuber as described by Schultz and Folsom (15). They state, in addition to the above symptoms, that spindle-tuber plants bloom more profusely and have more erect and more conspicuous flowers. They also note that "in very extreme cases" the tubers are sometimes ill-shaped and crooked and that the lenticels are numerous and large; that there is a tapering enlargement of the stolons, which are sometimes one-half inch in diameter at the point of attachment with the tubers; that some eyes never sprout and others sprout much later than normally, resulting in greatly delayed emergence. They also note the occurrence of rudimentary leaflets on the newly formed tubers late in the growing season.

Werner (12) discusses many of the symptoms previously mentioned in great detail. He states in addition that "spindle-tuber plants are shorter-lived than normal plants, when considering the number of days they are above ground." Werner used the width/length ratio of the tuber dimensions as the criterion for diagnosing the disease in the tubers and presents much of his experimental data on the basis of this ratio expressed in percentage terms. In discussing the change in color of the Triumph variety he states that "The color of the tubers is not a reliable guide for detecting the early stages of the disease."

Unmottled curly dwarf.—This disease was named and described by Schultz and Folsom (15) in 1923. They list the symptoms in the Green Mountain variety as consisting of

"pronounced dwarfing, spindliness, dark green color of the foliage early in the season, wrinkling, rugosity, slight ruffling, curling, some rolling, uprightness, brittleness, burning, somewhat premature death, and spindling, gnarled, and cracked tubers." They state that this symptom complex "has remained too true to type for three years to be considered yet as a combination of diseases, altho it may eventually be demonstrated to be such." They suggest the possible combination of leaf-rolling mosaic and spindle tuber with the masking of the mosaic mottling, but they also point out that in such combinations known as "mottled curly dwarf" the tuber symptoms as regards size and cracking are not as in "unmottled curly dwarf." They also transmitted the disease by leaf mutilation inoculations and by aphids, such inoculations always resulting in similar symptoms. The same authors (16) state that this appears to be a single disease and add that "The tuber cracking may appear, without the spindliness, as a symptom resulting from current season inoculation."

Folsom (3) tabulates the differential characteristics of eleven virus diseases of the potato. By comparing the tabulated symptoms of spindle tuber and unmottled curly dwarf it becomes evident that the difference is chiefly one of degree with a few additional related symptoms characterizing unmottled curly dwarf. He lists the darker green color, rigidity, spotting, and burning as being the same for both diseases. Dwarfing, spindliness, and wrinkling occur with both but are more distinct or extreme with unmottled curly dwarf. The slight rolling sometimes occurring with spindle tuber is not listed for unmottled curly dwarf. Curling, brittleness of stems and petioles, streaking, leaf dropping, tender leaf texture, and premature death are listed as occurring with unmottled curly dwarf but not with spindle tuber. In contrast with the premature death of unmottled curly dwarf, he lists spindle-tuber as being longer lived than normal plants. The tuber characters are given as being the same for both diseases with the addition of lengthwise growth cracks for unmottled curly dwarf. A further similarity of spindle tuber and unmottled curly dwarf is evident in regard to transmission, the only difference being the greater ease of transmitting unmottled curly dwarf by leaf mutilation. The above description, given by Folsom, was based upon the symptoms as they appeared in the Green Mountain variety. The necrotic symptoms of burning, spotting, streaking, and associated leaf dropping are often more severe with the Green Mountain than with the Triumph variety. Owing to the omission or slight occurrence of these symptoms in the Triumph, the similarity of the two diseases is more evident, the chief difference being

the degree of severity of the symptoms, which is shown in the effect upon yield listed by Folsom as being a 20 per cent reduction for spindle tuber and 60 per cent for unmottled curly dwarf.

Identity of the two diseases.—The above brief review of the descriptive literature clearly shows the similarity of the symptoms of these two diseases and the difficulty of distinguishing between them. With a variation in symptoms occurring in different varieties and in individual plants of the same variety, there is an overlapping of symptoms that makes it impossible in many instances to make an accurate diagnosis on the basis of the published descriptions. It is quite probable that both diseases have been studied under the name of spindle tuber and that unmottled curly dwarf has often been considered as severe spindle tuber. Werner (12, 13) refers to the progressive severity of spindle tuber in successive generations. His description of the disease, particularly in regard to tuber cracking, yield effects, and general severity of the symptoms, indicates that he was probably working with both diseases. The photographs of plants presented by Werner (13, Fig. 20, and 12, Fig. 7) show all the characteristics of unmottled curly dwarf as described by Schultz and Folsom.

The fact that these two diseases have many symptoms in common and have undoubtedly been considered sometimes as one disease, combined with the lack of any evidence corroborative of Schultz and Folsom's investigations, makes it desirable to discuss briefly at this point the possible relationship of the diseases and some of the results obtained by the author in investigations being prepared for a separate publication.

On the basis of symptoms alone, there is certainly a reasonable doubt as to whether unmottled curly dwarf is a separate and distinct disease or a modification of spindle tuber which is exhibited by a progressive increase in the severity of the symptoms. The author was strongly inclined to this view when the original description of unmottled curly dwarf was published by Schultz and Folsom (15). However, after some thousands of inoculations with both diseases, it became evident that each disease maintained its own characteristics upon transmission. Inoculation with the juice of unmottled curly dwarf has never given rise to spindle tuber nor has the reverse occurred. It is evident, therefore, that unmottled curly dwarf is not the result of a gradual and progressive increase in the severity of spindle tuber. This resembles the action of the mosaic diseases of the potato in retaining their characteristic symptoms in successive generations. It may be possible, however, that the spindle-tuber virus can be modified

in such a way as to produce a new set of symptoms, such as those of unmottled curly dwarf and that the virus thereafter transmits as unmottled curly dwarf. In order to prove this, it would be necessary to show the development of unmottled curly dwarf in the progeny of spindle-tuber plants, or by inoculation with spindle tuber under conditions which strictly exclude the possibility of uncontrolled transmission of unmottled curly dwarf by insect vectors or other means. There has been no indication of this occurring in the author's investigations, which involve large enough numbers to justify the conclusion that if such a modification of the virus occurs it is only in rare instances.

Distribution of unmottled curly dwarf.—It is interesting to note that Folsom (3) lists spindle tuber as being common in native stocks while unmottled curly dwarf is listed as being absent outside of the experimental plots. The author has found an abundant distribution of unmottled curly dwarf in commercial fields in Nebraska. Many of the poor lines of seed that were "running out" were found to contain unmottled curly dwarf. If Werner (12, 13) was working with both diseases, it is clearly evident that the disease occurred, not only in Nebraska but in a number of other states. It is possible that unmottled curly dwarf had been present for many years and had been described variously as leaf roll, curly dwarf, or just as run-out or "degenerate" plants. Orton (9), in 1914, referred to a western outbreak of leaf roll in the Greeley district of Colorado and in the Scotts Bluff section of Nebraska in 1911 and 1912. It is peculiar that during the last nine years the author has failed to find more than traces of leaf roll in the Scotts Bluff section, altho many fields of run-out stock have a high percentage of spindle tuber and unmottled curly dwarf. While the symptoms of leaf roll as described by Orton are typical of that disease rather than of unmottled curly dwarf, he states that in this outbreak in Colorado and Nebraska there were "more pronounced abnormalities in stolon and tuber formation than are described in the German literature." The photograph of tubers in Orton's publication (9, Plate XIII) shows the increased length and longitudinal cracking so characteristic of unmottled curly dwarf, which are not considered symptoms of leaf roll. It is probable that unmottled curly dwarf was present in 1910 and was confused to some extent with leaf roll or with curly dwarf, existing as a combination of several virus diseases.

ENVIRONMENTAL MODIFICATIONS OF SYMPTOMS

The author (4) in 1924 reported upon the effect of environmental factors on the symptoms of some of the potato virus diseases. While mosaic was the chief disease studied, notes

were also made regarding the development of spindle tuber. With three successive dates of planting in western Nebraska, it was found that the foliage symptoms were more severe with the later date. The cooler weather which prevailed during the early growth with the first plantings masked the symptoms of spindle tuber so that even with high temperatures later in the season the plants did not have severe symptoms. On the other hand, those that started growth under high temperature conditions, such as occurred with the late-planted lots, showed severe symptoms thruout the season. It was also evident from a study made under controlled conditions in the greenhouse that the tuber symptoms were more severe when the tubers developed at a temperature of 25° than at 15° C., and that the temperature previous to the time of tuber setting did not influence the tuber symptoms.

This work was continued in 1923 and 1924 and was reported by Goss and Peltier (6). With controlled conditions in the greenhouse, high soil temperatures increased the severity of the tuber symptoms of spindle tuber and high soil moisture tended to produce the same effect. The same factors caused an abnormal growth of the tubers of healthy plants, which tended to make them appear as if affected by spindle tuber. It was also found that the foliage symptoms of spindle tuber were intensified at high temperatures and masked at low.

Werner (12), using the elongation of the tuber expressed as width/length as a basis of comparison, reported that the tubers of spindle-tuber plants were not as elongated at low soil temperatures with low soil moistures and in light (sandy) soils as when the reverse conditions prevailed. He also reported from extensive observations that with earlier planting dates in the field, the symptoms of the tubers were more severe, and that this was correlated with the high soil temperatures which prevailed during the period of tuber formation.

As previously noted, the possibility that unmottled curly dwarf was present in the material used in the above-mentioned investigations made it desirable to repeat this work on a more extensive scale and to include both diseases for a comparative study. Because of the similarity of the two diseases, more detailed information concerning the individual symptoms than is reported above was considered desirable.

SYMPTOMS OCCURRING IN THE GREENHOUSE

Before discussing the effect of certain environmental factors on the symptoms under controlled conditions, it is advisable to consider the possible changes in the symptoms when plants are grown under glass as contrasted with the field symptoms.

One symptom common to both diseases as they occur in the

field is the prolonged period of dormancy, resulting in delayed emergence. It might be expected then, that the very short rest period allowable with early plantings of infected tubers in the greenhouse would alter to some extent the disease symptoms. This was tested by planting portions of infected tubers of both diseases and also of healthy control tubers on successive dates in the greenhouse.

Tubers from spindle-tuber plants were planted November 10, December 13, January 10, and February 12 and unmottled-curly-dwarf tubers were planted on the last three dates. One seed piece was cut from each tuber for planting on each date. The plants were grown in a greenhouse held at a temperature of 20° to 22° C. in clay pots with a soil moisture content optimum for plant growth. The symptoms appearing on each plant were recorded weekly.

There was little effect on the symptoms of spindle tuber. The first planting produced in general a weaker type of plant. The later plantings all produced larger plants that were often difficult to distinguish from healthy plants.

The unmottled-curly-dwarf plants, on the other hand, were greatly affected by time of planting. The December and January plantings produced plants that were quite similar to the spindle-tuber plants but with the last planting in February the symptoms were much more severe. Even tho planted two months later the plants were larger on the same date than the earlier plantings. They were more erect and the rumpling and twisting of the leaves was much more pronounced, as shown in Plate 1 C.

These results were typical of the effect of early planting in the greenhouse. It is usually very difficult to separate spindle-tuber and unmottled-curly-dwarf plants in early-winter plantings of potatoes harvested in September or October, as shown in Plate 1 A. With later planting the unmottled-curly-dwarf symptoms are more nearly like those which occur in the field (Plate 1 B). The spindle-tuber plants, however, are always difficult to detect, and the author has found it impossible always to diagnose accurately the disease in the greenhouse from the vine symptoms. In all index work and experiments dealing with spindle tuber, it has been found necessary to keep the plants until the new tubers are formed and to base the diagnosis upon both tuber and vine symptoms. The tuber symptoms are usually distinct, and infected tubers can be separated quite readily from healthy tubers grown at the same time. The eye characters and the extreme decrease in color are the most evident symptoms in the greenhouse.

In the greenhouse the leaves are smoother than is normal and often more pointed, with a slight tendency to roll down-

ward. The blossoms of both spindle-tuber and unmottled-curly-dwarf plants are more conspicuous, occurring earlier than in the field. Infected plants sometimes blossom in the greenhouse when only 6 to 8 inches high. If seed tubers have gone thru the normal period of dormancy, the infected plants are more easily identified while young than after they are several months old.

THE EFFECT OF SOIL MOISTURE ON THE SYMPTOMS

Soil moisture is one of the most variable environmental factors influencing the production of potatoes. This is especially true in the dry-land sections where rains are often of local occurrence and vary greatly from year to year. The differences in soil texture and topography result in a wide variation in the moisture content of neighboring fields and even within individual fields. The type of plant growth and tuber development is greatly influenced by this variable moisture content and it is often quite difficult to differentiate between healthy and spindle-tuber plants. Previous to the description of unmottled curly dwarf, it had been thought that this symptom complex, called severe spindle tuber, was due to the effect of soil moisture and other factors on the development of the symptoms of spindle tuber. It was therefore of interest to determine whether or not soil moisture could affect the symptoms of these two diseases to a great enough degree to cause serious confusion in their diagnosis.

The results of a test conducted in 1924 are presented in Table 1. Tubers were selected from Bliss Triumph plants showing symptoms of spindle tuber in varying degrees of severity. All the plants were selected from the same experimental plot. No authentic unmottled curly dwarf was available but the plants selected as severe spindle tuber checked quite well with the symptoms of unmottled curly dwarf as described by Schultz and Folsom (15). The tubers from these plants also showed more severe symptoms (Table 1). The tubers were cut into seed pieces of equal weight and planted in soils with moisture contents of ⅔, 1, and 1½ times the soil moisture equivalent, which was 17.6 per cent dry weight. The experiment was planted November 24 from seed dug in late September and was conducted in a greenhouse held at a temperature of about 22° C.

In 1927 the experiment was repeated with seed tubers of known history and the results are given in Table 2. The seed tubers used in this test are shown in Plate 2. The unmottled-curly-dwarf tubers were from the second generation of Bliss Triumph plants, which had been inoculated from unmottled-curly-dwarf Green Mountains obtained from Schultz and Folsom. Two unmottled-curly-dwarf tubers

TABLE 1.—*The effect of soil moisture on the symptoms of spindle tuber and unmottled curly dwarf, 1924-25*

Soil moisture equivalent [1]	Healthy [2]	Spindle tuber [2]	Unmottled curly dwarf [2]
	Number of sprout tubers formed		
⅔	0	0	10
1	0	0	2
1½	0	0	5
	Average number days to emergence		
⅔	19	35	16
1	9	21	29
1½	9	21	22
	TUBER SYMPTOMS		
	Increase in length as L/W ratio		
⅔	.881	.934	1.036
1	.999	1.097	1.059
1½	1.173	1.195	1.332
	Decrease in color		
⅔	None	Very slight	Very slight
1	Very slight	Slight	Medium
1½	Slight	Slight to medium	Severe
	Increase in number and shallowness of eyes		
⅔	None	Very slight	Slight
1	Very slight	Slight to medium	Medium
1½	Slight	Medium	Severe
	Combination of all symptoms		
⅔	None	Very slight	Slight
1	Very slight	Slight to medium	Medium
1½	Slight	Medium	Severe.

[1] The moisture equivalent of the soil used in this experiment was 17.6 per cent dry weight.

[2] The following numbers of plants were used respectively at the 2/3, 1, and 1 1/2 soil moisture sets: healthy 10, 5, and 10; spindle tuber 8, 4, and 8; unmottled curly dwarf 12, 6, and 12.

The L/W ratio of the seed tubers and their appearance were as follows:
Healthy, L/W = 1.075, normal appearance.
Spindle tuber, L/W=1.218, symptoms of medium severity.
Unmottled curly dwarf, L/W = 1.604, symptoms very severe.

TABLE 2.—*The effect of soil moisture on the symptoms of spindle tuber and unmottled curly dwarf, 1927-28*

Soil moisture equivalent [1]	Healthy [2]	Spindle tuber [2]	Unmottled curly dwarf [2]
	Average number of days to emergence		
⅔	34	41	43
1	25	31	34
1⅓	18	34	32
	Average length of life from emergence (days)		
⅔	104	97	82
1	119	108	98
1⅓	107	95	90
	Average length of life from planting (days)		
⅔	134	138	125
1	144	139	132
1⅓	125	129	122
	Average total weight of tubers per plant (grams)		
⅔	193	81	48
1	398	110	75
1⅓	308	66	64
	TUBER SYMPTOMS		
	Increase in length		
⅔	None	Very slight	Slight to medium
1	Slight	Medium	Slight to medium
1⅓	Medium	Medium to severe	Medium to severe
	Decrease in color		
⅔	None	Very slight	Slight
1	Slight	Medium	Slight to medium
1⅓	Medium	Medium to severe	Medium
	Increase in number and shallowness of eyes		
⅔	None	Slight	Slight to medium
1	Very slight	Medium	Medium
1⅓	Slight	Medium to severe	Medium
	Cracking		
⅔	None	None	Very slight
1	None	None	Slight to medium
1⅓	None	None	Slight
	Combination of all symptoms		
⅔	None	Very slight to slight	Slight to medium
1	Very slight	Medium	Medium
1⅓	Slight to medium	Medium to severe	Medium

[1] The moisture equivalent of the soil used in this experiment was 30 per cent dry weight.

[2] Five healthy, five spindle-tuber, and fifteen unmottled-curly-dwarf plants were grown at each soil moisture.

(Plate 5 A-2, 3) were also used from plants inoculated in the summer of 1927. The moisture equivalent of the soil used was much higher than in the previous experiment, being 30 per cent dry weight, so the three moisture sets were made up at 20, 30, and 40 per cent dry weight, equal to ⅔, 1, and 1⅓ M. E. The experiment was started about two weeks earlier than the previous test.

One of the most constant symptoms of spindle tuber and unmottled curly dwarf is the increased length of the dormant period as shown by the delayed emergence of plants. In these experiments there was but little difference between spindle tuber and unmottled curly dwarf, both requiring considerably more time to emerge than the healthy plants. There was no great difference between the medium and high soil moisture sets but with the low moisture, emergence was greatly retarded. The exception with unmottled curly dwarf in the 1924 experiment (Table 1) was probably due to the small number of plants, as only two emerged in this set and the figures are not so reliable. The greater length of time for emergence with all sets in the 1927 experiment (Table 2) was probably due to the later harvesting and earlier planting of the experiment as compared with the 1924 test.

In addition to the retarded emergence, there were 17 seed pieces from the unmottled-curly-dwarf tubers that failed to produce plants in 1924 (Table 1). When the seed pieces were dug up for examination, it was found that in every instance the sprouts had abnormally developed into tubers (Plate 5 A-1). This abnormal tuber development was distinctly correlated with the severe symptoms of unmottled curly dwarf in the seed tubers. There was no instance of its occurrence with healthy or spindle-tuber seed. There was a greater proportion of such abnormal tuber development with low soil moistures. This abnormal sprout growth did not occur in the 1927 tests.

The chief effect of soil moisture on the vine growth was to produce a more rapid luxuriant growth with a high soil moisture content. The vine symptoms of spindle tuber and unmottled curly dwarf commonly occurring in the field were almost entirely absent in these greenhouse tests. During the early stages of growth there was very little difference between the spindle-tuber and unmottled-curly-dwarf plants. Both were smaller than the healthy plants but this was chiefly due to the later emergence. In the 1927 test, many of the spindle-tuber and unmottled-curly-dwarf plants were chlorotic when they emerged and were distinctly brittle with smooth, round leaves. This was correlated with the retarded emergence and has been observed by the writer to occur in the field with healthy plants that were retarded due to unfavorable soil con-

ditions. The chlorotic symptoms are, therefore, not of great diagnostic value in detecting these diseases. After the plants were four inches in height they lost this chlorotic appearance and were more erect with an acute angle of branching.

In the later stages of growth the spindle-tuber plants were considerably dwarfed in comparison with the healthy at the low and medium moisture contents. In the high moisture set they eventually became as tall as the healthy plants but were weaker and more spindly. They did not exhibit any ruffling or twisting of the leaves. The unmottled-curly-dwarf plants a month after emergence could be distinguished from the spindle-tuber in only two ways. With a high moisture content they were slightly more dwarfed than the spindle-tuber plants, they had a more erect appearance due to the acute angle of branching, and the leaves were distinctly ruffled with a twisting of the terminal leaflets. With a lower moisture content the plants were quite similar to spindle tuber but were often more spindly, with a weaker type of growth (Plate 3 A). There was considerable variation in the type of vine growth of individual plants in this experiment and it would have been impossible in many instances to make a correct identification of the disease.

In the 1927 experiment a record was kept of the length of life of each plant in the experiment. Folsom (3) lists spindle-tuber plants as being longer lived than healthy, whereas unmottled curly dwarf is characterized by premature death. While spindle-tuber plants often appear to be longer lived in the field, the writer has always considered that this was due to the delayed emergence and that they can only be considered to be longer lived if the planting date is taken as the basis for comparison rather than the date of emergence. Folsom does not state which basis he used for comparison, but judging from the data here presented in Table 2, he was considering the length of life in relation to planting date. When the date of planting was used as a basis, practically no difference was found between healthy and spindle-tuber plants, the spindle tuber being slightly longer lived at the low and high moistures and the healthy at the medium moisture content; the unmottled-curly-dwarf plants, however, were shorter lived with all soil moistures. When the date of emergence was taken as the basis both spindle-tuber and unmottled-curly-dwarf plants died prematurely.

Both healthy and infected plants in the medium soil moisture set were distinctly the longest lived and produced the greatest weight of tubers (Table 2). The effect of the two diseases on yield and the more serious reduction caused by

unmottled curly dwarf were clearly evident even with this small number of plants grown under greenhouse conditions.

The severity of the tuber symptoms increased with an increased soil moisture content (Plate 3 B, C, D). As indicated in Tables 1 and 2, the tubers were longer, the color was paler, and the number and shallowness of the eyes were greater with a high soil moisture. The ratio of length to width given in Table 1 for the 1924 test clearly shows the effect of soil moisture on the length of both healthy and infected tubers. The figures for the unmottled curly dwarf are not so consistent, probably owing to the smaller number of plants, but the effect of the soil moisture and the increased length as compared with spindle tuber are evident in the data for the low and high soil moisture sets.

The tubers produced by spindle-tuber plants with a low soil moisture appeared quite normal. There was a slight increase in the number and shallowness of eyes and a slightly blotched color, evident only by a close comparison with healthy tubers produced under similar conditions. The shape of the tubers was normal and the L W ratio failed as a criterion for diagnosing the disease. With a higher soil moisture the increased length and the paler color were the more prominent symptoms.

The tuber symptoms of unmottled curly dwarf were quite similar to those of spindle tuber, individual tubers often being indistinguishable as regards symptoms. In general, the unmottled-curly-dwarf tubers were slightly more elongated. They were most easily distinguished from spindle tuber in the low soil moisture set where the unmottled-curly-dwarf tubers showed slight but distinct symptoms. While no cracking occurred in the 1924 test, in 1927 the unmottled-curly-dwarf tubers showed distinct longitudinal cracks at all soil moistures but more severely in the high moisture set. The effect of soil moisture on the length, color, and eye characteristics was very similar to that occurring with spindle tuber.

In the 1927 tests the unmottled-curly-dwarf tubers showed a slight surface necrosis centering around the lenticels (Plate 5 B-1). This necrosis was quite severe in the high moisture set, slightly less in the medium moisture set, and did not occur in the low moisture set. This necrosis did not occur with spindle-tuber or healthy tubers nor did it occur in the 1924 tests sufficiently to be noted. It increased in severity after the tubers were placed in cold storage and the injury appears to be quite similar to that described by Wright and Peacock (14) as occurring around the lenticels when immature potatoes are stored at 32° and 36° F. In this experiment the injury started previous to storage and increased in storage at 36° to 38° F. for one week, after which no further increase was noted.

TABLE 3.—*The effect of soil temperature on the symptoms of spindle tuber and unmottled curly dwarf, 1924-25*

Soil temperature degrees centigrade [1]	Healthy [2]	Spindle tuber [2]	Unmottled curly dwarf [2]
	Average number of days to emergence		
15	11	20	26
20	11	19	79
25	11	13	14
30	12	14	10
	TUBER SYMPTOMS		
	Increase in length as L/W ratio		
15	1.024	1.029	1.493
20	1.177	1.401	No tubers
25	1.085	1.704	1.482
30	1.340	1.576	1.727
	Decrease in color		
15	Slight	Slight	Medium
20	Very slight	Slight to medium	
25	Medium	Medium	Severe
30	Medium	Medium	Very severe
	Increase in number and shallowness of eyes		
15	Very slight	Slight	Medium
20	Slight	Medium to severe	
25	Slight	Medium to severe	Severe
30	Medium	Severe	Severe
	Combination of all symptoms		
15	Very slight	Very slight	Medium
20	Slight	Medium	
25	Medium	Severe	Severe
30	Severe	Severe	Very severe

[1] Three additional sets at a soil temperature of 15° with air temperature of 20°, 25°, and 30° produced tubers similar to those listed at 15° C. and are therefore omitted from the table.

[2] Three healthy, three spindle-tuber, and two unmottled-curly-dwarf plants were grown at each temperature.

The L/W ratio of the seed tubers and their appearance were as follows:
Healthy, L/W = 1.083.
Spindle tuber, L/W=1,403.
Unmottled curly dwarf, L/W = 1.912.

It is important to note that the tubers produced on healthy plants at high soil moistures look more like spindle tuber than those from the spindle-tuber plants produced with a low soil moisture. When these tubers were placed on a table with no notation regarding the conditions under which they were produced, it was found impossible to separate healthy and infected tubers or to determine whether they were spindle-tuber or unmottled-curly-dwarf tubers. The difficulty of diagnosing spindle-tuber plants under high soil moisture conditions is offset by the fact that under these conditions the tubers show the most distinct symptoms.

The variation in the occurrence of individual symptoms, such as the L W ratio, is so great that it is essential to consider all possible symptoms. It is impossible, even when all symptoms are considered, to distinguish the several diseases when tubers grown under different conditions are compared or when the conditions are not known.

THE EFFECT OF TEMPERATURE ON THE SYMPTOMS

It has been shown by Goss and Peltier (6) and by Werner (12) that the soil temperature changes the tuber symptoms of spindle tuber and modifies the characteristics of healthy tubers. There has been no evidence presented regarding unmottled curly dwarf and this disease may have been present in some of the experiments dealing with spindle tuber. It was therefore desirable to determine the effect of both the soil and air temperature in relation to these two diseases.

In 1924 an experiment was undertaken using seed potatoes from the same sources as for the soil moisture experiment (p. 12). The soil was similar to that used in the soil moisture experiments conducted the same years and the moisture was kept at a content equal to the soil moisture equivalent. By the use of soil temperature tanks combined with air temperature cases (10), different combinations of air and soil temperatures were obtained. The results are presented in Table 3. Four different air temperatures, 15°, 20°, 25°, and 30°, were used with a soil temperature of 15° C. In the same experiment three sets were used with an air temperature of 15° and a soil temperature of 15°, 20°, 25°, and 30°.

It was found that high air temperatures modified the foliage symptoms by causing a taller, more spindly, more etiolated type of growth. The upright, erect appearance of infected plants was intensified in many plants, particularly at 25° C. At 30° a weaker type of growth predominated. Sometimes with a high air temperature the ruffling of the leaves was increased, especially at 25° and 30°. The leaves were longer, narrower, smoother, and more pointed, with a tendency to roll downward. The temperature of the air did not have any

effect upon the symptoms of the tubers other than a reduction in yield with the highest air temperatures. For this reason the results presented in Table 3 and in the following discussion do not include the three sets with different air temperatures.

In 1927 another test was made using unmottled-curly-dwarf and spindle-tuber seed of known history from the same plants as the seed used in the 1927 soil moisture test. Four different soil temperatures were used but the air temperature cases were not used as in the previous test. The experiment was conducted at a greenhouse temperature of about 22° C. Otherwise, the test was conducted in the same manner as in 1924. The results are presented in Table 4.

In these soil temperature experiments both spindle tuber and unmottled curly dwarf again delayed emergence, particularly at 15° C., where the healthy plants were also slow in emerging. There was not as great a difference in the time required for emergence with the different soil temperatures as in the previous experiments with soil moistures. In the 1924 test abnormal development of the sprouts again occurred with the unmottled curly dwarf plants. Seven of the 14 seed pieces planted produced sprout tubers, as in the soil moisture tests, but there was no correlation with the different soil temperatures. This abnormal sprout development did not occur in the 1927 experiment.

The difference in the type of growth produced at different soil temperatures was even greater than that occurring with different air temperatures. At all temperatures the healthy plants were the largest and the difference between healthy and spindle-tuber plants was only slight, particularly at the lower temperatures. The unmottled-curly-dwarf plants were severely dwarfed and could be easily detected, particularly in the later stages of growth, at all temperatures.

At 15° C. both the spindle-tuber and unmottled-curly-dwarf plants appeared quite normal until they were about 6 inches high, the chief difference between healthy and infected plants being evident in size. When the healthy plants were 15 inches tall none of the infected plants was more than 3 inches in height. In the later stages of growth the infected plants developed slight symptoms which were never as distinctive as at the higher temperatures, the spindle-tuber plants being especially difficult to distinguish from the healthy. At 20° the symptoms were only slightly more severe than at 15° and the relative differences between healthy and infected plants remained about the same.

The plants grown at soil temperatures of 25° and 30° C. were in marked contrast to those produced at the two lower temperatures. At these high temperatures both the spindle-

TABLE 4.—*The effect of soil temperature on the tuber symptoms of spindle tuber and unmottled curly dwarf, 1927-28*

Soil temperature degrees centigrade	Healthy [1]	Spindle tuber [1]	Unmottled curly dwarf [1]
	Average length of life from planting (days)		
15	138	135	137
20	130	133	123
25	112	107	92
30	96	81	81
	Average weight of tubers per plant (grams)		
15	253	36	94
20	256	59	37
25	205	16	10
30	121	5	10
	TUBER SYMPTOMS		
	Increase in length		
15	None	Very slight	Very slight
20	Slight	Slight to medium	Slight to medium
25	Medium	Medium	Medium
30	Medium	Medium	Medium
	Decrease in color		
15	None	Slight	Slight
20	Very slight	Slight to medium	Slight
25	Slight to medium	Slight to medium	Medium
30	Severe	Severe	Severe
	Increase in number and shallowness of eyes		
15	None	Slight	Slight to medium
20	Slight	Slight to medium	Medium
25	Medium	Medium to severe	Medium to severe
30	Medium to severe	Medium	Medium
	Combination of all symptoms		
15	None	Slight	Slight
20	Slight	Slight to medium	Slight to medium
25	Medium	Medium	Medium
30	Medium to severe	Medium to severe	Medium to severe

[1] Four healthy, four spindle-tuber, and eight unmottled-curly-dwarf seed pieces were planted at each soil temperature.

tuber and unmottled-curly-dwarf plants were chlorotic with wrinkled and brittle leaves until they were about 4 inches high. Thereafter, the spindle-tuber plants were slightly dwarfed and erect with smooth, pointed leaves slightly ruffled and with the terminal leaf twisted. The spindle-tuber plants at 25° were quite similar to the unmottled-curly-dwarf plants at 20°. The unmottled-curly-dwarf plants developed into very erect plants with an acute angle of branching. They became severely dwarfed, with darker green, smaller leaves and with more ruffling and twisting than the spindle-tuber plants. At 30° the symptoms were more severe than at 25°. At this high temperature the healthy plants were also more erect with smooth, pointed leaves, but were more easily distinguished from the infected plants than at the low temperatures, due to the severity of the symptoms on infected plants, particularly the unmottled curly dwarf.

The length of life of all plants was much shorter at 25° and 30° C. than at the lower soil temperatures. Unmottled-curly-dwarf plants were slightly shorter-lived at all temperatures above 15°. In general there was a distinct increase in the severity of all symptoms with an increase of soil temperature. At 15° and 20° the symptoms were very slight, while at 25° and 30° they were severe (Plate 4 C).

The detailed notes on tuber symptoms are presented in Tables 3 and 4. The differences between the healthy and infected tubers and between sister plants at different temperatures were for some reason more evident in the 1924 experiment than in 1927. This may have been due to the fact that a richer soil with a higher moisture equivalent was used in the 1927 experiments. In both experiments, however, there were marked differences due to the soil temperature. The spindle-tuber and unmottled-curly-dwarf tubers were indistinguishable in the 1927 test and could be separated from the healthy only by the lighter color. Both the spindle-tuber and unmottled-curly-dwarf tubers at 15° were quite normal in appearance, while at 20° C. they were slightly longer than normal and with more numerous shallow eyes. At 25° and 30° the elongation and decreased color were the most noticeable symptoms. Cracking occurred with only one unmottled-curly-dwarf tuber. In 1924 the average unmottled-curly-dwarf tuber was slightly lighter in color, with a slight insrease in number and shallowness of eyes as compared with spindle tuber.

The healthy tubers at 15° were normal in appearance while at 20° C. they were slightly more elongated with a larger number of shallow eyes and a paler color. These changes in the normal appearance increased at the higher temperatures. At

30° the tubers were a pale cream color and appeared about the same as typical spindle tuber.

The most noticeable effect of the soil temperature was the abnormal appearance of the healthy tubers at the high temperatures and the absence of symptoms in the infected tubers at 15° C. If the tubers had been examined separately without a knowledge of the conditions under which they had been grown, the healthy checks at 25° and 30° would have been listed as spindle tuber and the infected tubers grown at 15° would have been judged healthy.

There was found to be a considerable difference in the symptoms of individual tubers produced by different plants under the same conditions and sometimes of different tubers from the same plant. The difference between the 1924 and the 1927 tests also indicated that factors other than soil temperature might modify the symptoms even when the tests were made under controlled conditions as in these experiments. No one symptom, such as the L/W ratio, was found that could be relied upon for diagnosing either disease or to distinguish between spindle tuber and unmottled curly dwarf. It is necessary to use all symptoms combined and even then it is essential to compare the infected and healthy tubers produced under similar conditions as can be noted in Plate 4 A, B.

RELATION OF THE DISEASES TO SPROUT DEVELOPMENT

Development of sprout tubers.—It has been noted in the soil moisture and temperature experiments that unmottled-curly-dwarf tubers will sometimes form sprout tubers and that this development is apparently favored by a low soil moisture content. This effect of environment is similar to the results reported by Weiss and Brierly (11) regarding the development of sprout tubers from healthy potatoes. In these experiments, however, only the unmottled-curly-dwarf tubers produced sprout tubers and the seed tubers were grown and stored under the same conditions as were the healthy and spindle-tuber seed. It is evident, therefore, that unmottled-curly-dwarf seed is more susceptible to unfavorable soil conditions and has a greater tendency to produce sprout tubers. The author (5) previously reported this abnormal sprout development as being correlated with spindle tuber, but this report was made previous to the differentiation of spindle tuber and unmottled curly dwarf and a further study of the seed stock used in that experiment showed conclusively that the severe spindle tuber referred to was undoubtedly unmottled curly dwarf. The sprout tubers were formed (Plate 5 A-1) directly from the eye of the mother tuber without the production of an intermediate sprout. In many instances, the

sprout tuber actually weighed more than the mother seed piece. In no case did secondary sprouts arise from these sprout tubers when left in the soil for two months, altho they were capable of producing a weak type of plant when replanted after a sufficient rest period. This development of sprout tubers is not considered by the author to be of great importance in field plantings, but is an example of the effect of a virus disease in predisposing a tuber to abnormal sprout development under unfavorable conditions.

Apical dominance.—The relation of spindle tuber or unmottled curly dwarf to apical dominance has not been mentioned by other workers, so far as the writer is aware. Repeated tests have shown that tubers affected with either disease tend to lose the factor for apical dominance, and that all the eyes develop sprouts of a rather weak type. The type of development of spindle-tuber sprouts as contrasted with healthy is shown in Plate 5 C; the tubers illustrated were grown in the same field and kept in the same cold storage. The author at one time thought that this lack of apical dominance might be employed as a basis for sorting out infected seed before planting. Repeated trials, however, have shown that while lack of apical dominance often occurred with seed infected with either of these diseases, the same thing was sometimes true of healthy seed. Apical dominance, therefore, could not be used to separate infected from healthy seed, at least with the Triumph variety under western Nebraska conditions.

The effect of chemical treatments.—Various chemical treatments have been used to break the rest period of dormant healthy potatoes and this method is often employed for early winter indexing of seed stock. The purpose of such indexing usually is to detect infected tubers and therefore it is of importance to know the possible effect of these treatments upon the development of disease symptoms. Inasmuch as the two diseases being considered are characterized by retarded emergence in the field as a result of an abnormally long rest period and are also subject to other sprout abnormalities, as previously indicated, it was of particular interest to determine the physiological response of infected seed to various treatments.

In all of the following tests on sprout development, the factor of maturity was not considered. Infected and healthy tubers which had been dug at the same time and stored for the same period were used. Due to their characteristic late emergence in the field and later development, the tubers from spindle-tuber plants may have been more immature than the healthy and this may have been a contributing factor in the

results reported. Nevertheless, the disease was the original factor causing this possible immaturity and the following tests and discussion are based solely upon infected and healthy seed handled in a similar manner.

In 1925 tubers were selected from healthy and spindle-tuber plants and stored at 2° to 3° C. for one month. Twenty tubers of each were selected and each tuber cut into four seed pieces, all seed pieces being of approximately the same weight. The four seed pieces were treated as indicated in Table 5, and planted in moist sand at a temperature of 20° to 25°. They were examined four weeks after treating and notes made on the condition of the seed pieces, sprouts, and roots.

Spindle tuber greatly retarded the sprouting of seed pieces as seen by a comparison of the untreated checks of both healthy and spindle tuber. The sodium nitrate was much more effective than potassium permanganate in breaking the rest period, altho both accelerated sprouting of healthy tubers. When potatoes were infected with spindle tuber, they responded in a lessened degree to these treatments, the potassium permanganate being ineffective, while sodium nitrate was effective but much less so than with healthy tubers. The most remarkable results were obtained by placing the seed pieces in an air-tight container. With healthy tubers, nineteen of the twenty seed pieces rotted, while only one of those infected rotted and all of the others sprouted when placed in sand. This treatment was much more effective in breaking the rest period of infected tubers and stimulating growth than either of the chemical treatments. This action is undoubtedly tied up with respiration, either the lack of oxygen or the excess carbon dioxide having the effect of breaking dormancy.

Keeping the seed tubers in a closed container for seven days was so effective in breaking the rest period of spindle tubers that another experiment was made the following year. Healthy and spindle-tuber potatoes harvested in September were kept in cold storage until November 27 and then were cut into equal size seed pieces and placed in closed containers (desiccators) at 25° and 3° to 5° with an equal number of checks left in the open at 25° C. The results presented in Table 6 show that holding spindle-tuber seed tubers in a closed container at 25° for seven days greatly stimulated sprouting but the same treatment at 3° to 5° was not effective. With healthy tubers held in a closed container at 25° considerable blackheart developed, five out of six seed pieces being affected, and of the 20 seed pieces planted, 13 rotted, probably due to blackheart.

Another experiment was conducted in a manner similar to the above, except that whole seed instead of cut seed was used

TABLE 5.—*The effect upon spindle-tuber and healthy seed pieces of treatments to accelerate sprouting, 1925-26*

Treatment of seed pieces	Development 4 weeks after planting										
	Seed piece rot	Average number sprouts per seed piece	Average length of sprouts	Vigor of sprouts[1]				Vigor of roots[1]			
				0	1	2	3	0	1	2	3
	Number	*Number*	*(mm.)*								
HEALTHY[2]											
A—.02 M. $KMnO_4$—40 min.	0	1.4	8.4	0	8	4	8	11	2	0	7
B—.5 M. $NaNO_3$ in .05 N. HC1—40 min.	0	1.1	26.7	0	0	3	17	3	0	2	15
C—Sealed container—7 days	19	2.0	60.0	0	0	1	0	0	0	0	1
D—No treatment	0	.7	2.9	8	1	1	10	18	1	0	1
SPINDLE TUBER[2]											
A—.02 M. $KMnO_4$—40 min.	0	.1	2.0	18	1	0	0	19	0	0	0
B—.5 M. $NaNO_3$ in .05 N. HC1—40 min.	2	.3	1.2	12	3	2	0	15	1	1	0
C—Sealed container—7 days	1	1.3	17.6	0	11	6	1	9	3	6	0
D—No treatment	1	0	0	18	0	0	0	0	0	0	0

[1] 0 = no growth, 3 = greatest vigor.

[2] Twenty healthy and 19 spindle-tuber seed pieces were used in each set. Those that rotted are not figured in the data on vigor.

TABLE 6.—*The effect of lack of aeration on the sprouting of healthy and spindle-tuber seed pieces*

Treatment of seed pieces	Occurrence of black heart 3 days after removal from container		Effect on sprouting 25 days after being placed in moist soil				
	Number seed pieces	Black heart	Total seed pieces	Seed pieces rotted	Dormant seed pieces	Seed pieces sprouted	Average height of sprout
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Inches*
HEALTHY							
Closed container 7 days at 25°C	6	5	20	13	0	7	1.1
Closed container 7 days at 3 to 5°C	6	0	20	6	0	14	1.0
Open container at 25°C	.	..	20	6	1	13	0.7
SPINDLE TUBER							
Closed container 7 days at 25°C	6	0	20	1	3	16	0.6
Closed container 7 days at 3 to 5°C	6	0	20	0	20	0	...
Open container at 25°C	..	..	12	0	9	3	0.2

and the experiment conducted at 5° C. No differences were noted in the development of the sprouts. Apparently the use of whole tubers instead of cut seed pieces and the low temperature used decreased the rate of respiration so that there was no accelerating effect on sprouting in the elapsed time.

Another test was made in 1927. The experiment was started on November 2 with potatoes harvested in September. Healthy, spindle-tuber, and unmottled-curly-dwarf seed was used, both cut and uncut, in closed containers at 25° C. for periods of 5, 10, 15, and 20 days. No differences were observed between the whole and cut tubers or between healthy and infected tubers in the set held for 5 days, nor did the treatment accelerate sprouting. With 10-day and 15-day exposures, all of the spindle-tuber seed rotted. The whole healthy tubers sprouted earlier with a 10-day exposure than with any of the other treatments, while all of the cut tubers with the same treatment rotted. None of the unmottled-curly-dwarf tubers rotted with these exposures and the most rapid sprouting occurred with the cut tubers held for 15 days. With a 20-day exposure all the eyes of the healthy tubers were dead when removed from the container, while all of the spindle-tuber cut tubers sprouted early. The results were rather confusing, particularly with spindle tuber, and the only conclusions to be drawn are that 5 days' exposure at 25° does not greatly affect the rest period, that 20 days' exposure kills the eyes of healthy tubers and that the rate of respiration with unmottled curly dwarf and spindle tuber is so low that a 20-day exposure simply accelerates sprouting. With cut tubers the rate of respiration is increased and sprouting is accelerated.

A further test was made by treating seed pieces of healthy and spindle-tuber potatoes with ethylene chlorhydrin about six weeks after harvesting. The treatment consisted of dipping cut seed tubers in a 5 per cent solution, draining, and placing in a closed container for 24 hours at about 20° C.

The ethylene chlorhydrin treatment of healthy seed had only a slight effect on the rate of emergence, decreasing the average time from 24 to 21 days. The treated seed pieces, after 60 days, were found to be more rotted than the untreated lots. The treatment of potatoes affected with spindle tuber greatly accelerated sprouting and obscured the delayed emergence characteristic of the disease. The average number of days required for emergence was reduced from 35 to 24 days, the treated spindle-tuber seed emerging at the same time as the untreated healthy. While the average of treated spindle tuber was three days longer than the treated healthy, this could not be applied to individual plants, due to variation

in the time of emergence. The degree of seed-piece rotting was greater with the treated than with the untreated, but less with healthy than with spindle-tuber seed. The more rapid emergence of the treated spindle-tuber seed was directly reflected in the earlier set of tubers on the plants.

The only differences noted in symptoms were with two untreated spindle-tuber plants which were quite chlorotic immediately after emergence, while the treated plants from the same seed tubers failed to show this chlorotic character. Also, the treated plants were generally larger and greener, and this made the detection of spindle-tuber symptoms difficult.

Attempts to identify the diseases by chemical tests.—Because of the difficulty of diagnosing spindle tuber on the basis of symptoms and the absence of methods of isolating the causal factor for identification, a quick and accurate chemical test would be highly desirable. The author has tried many different tests but without success. While qualitative tests for oxydase and catalase indicated that they were present in larger quantities in healthy than in infected tubers, the difference was too slight to warrant further work. Qualitative tests for nitrites were negative with both healthy and spindle-tuber potatoes but the diphenolamine test for nitrates indicated that more nitrates were present in spindle-tuber than in healthy potatoes. Accordingly, a large number of tests were made for nitrates with different lots of seed at different periods after harvesting and the following conclusions are based entirely upon the results obtained by using diphenolamine and estimating the relative amount of nitrates by the intensity of the blue color. A total of several thousand tests were made on more than five hundred tubers.

It was found that after potatoes had been in cold storage for six months or more the healthy tubers showed no nitrates, or only a slight amount, while the spindle-tuber potatoes were always positive and gave a very deep blue color. Healthy and spindle-tuber potatoes tested shortly after harvest, however, did not give any consistent differences, and the tests always indicated a higher concentration of nitrates than after a storage period. Both healthy and infected tubers varied considerably in the color reaction from different portions of the same tuber, the most consistent results being obtained by using small portions of the skin scraped off with a scalpel. After a winter's storage the bud ends did not show as high a concentration of nitrates as the stem ends. Positive nitrate tests were obtained with spindle-tuber potatoes even after the sprouts had developed, while with healthy tubers such tests were usually negative.

Nitrate tests of the foliage were rather inconsistent, altho spindle-tuber leaves usually showed a lower concentration of nitrates than healthy, and occasionally gave negative tests.

While such tests indicate that there is considerable difference in the nitrate content of spindle-tuber and healthy tubers, the test cannot be applied practically because of the variation occurring with healthy tubers even after a storage period when the differences are greatest. The decrease in the nitrate content of healthy tubers thru the storage period and during sprout formation, particularly at the bud end where the sprouts first start growth, shows that the nitrates are probably being used up in the formation of sprouts. The continued presence of nitrates in spindle-tuber potatoes after storage and sprouting indicates that the nitrates, for some reason, are not used in the same manner and this appears to be correlated with the symptom of delayed sprouting and the production of a weaker type of plant, particularly previous to extensive root formation when the young plant is normally drawing its food from the seed piece.

The purpose of this paper is not to present evidence or discuss the effect of these diseases upon the chemical composition of the plants. The preliminary qualitative tests reported, however, indicate that a quantitative chemical investigation of infected plants and tubers would yield much interesting information concerning the effect of the virus on the metabolism of the host.

THE DIFFERENTIAL VALUE OF THE SYMPTOMS

The author, for a number of years, has made observations in the field of the symptoms of spindle-tuber and unmottled-curly-dwarf plants of known history. The descriptions of these diseases in the Green Mountain variety by Schultz and Folsom (15) in 1923, supplemented by their additional notes in more recent papers, are closely paralleled by the symptoms shown on Bliss Triumphs under western Nebraska cultural conditions. It will be noted that some of the symptoms described for the Green Mountain variety by Schultz and Folsom (15) have been somewhat modified in Table 7 and that a few additional symptoms have been added.

Many of the symptoms given by Werner and Howard (13) and by Werner (12) were found to be more typical of unmottled curly dwarf than of spindle tuber, and it is quite evident that their references to cases of severe spindle tuber were descriptive of unmottled curly dwarf. While they list many additional characteristics in addition to those of Schultz and Folsom that are of considerable aid in identifying one or both of these diseases, it was noted that many of these symp-

TABLE 7.—*Description of the symptoms of spindle tuber and unmottled curly dwarf with their relative diagnostic importance on vines and tubers*

VINE SYMPTOMS	Spindle tuber		Unmottled curly dwarf	
	Order of relative value	Severity	Order of relative value	Severity
Spindliness—lateral dwarfing, slenderness	1	Distinct	4	Distinct
Uprightness—acute angle of branching	2	Distinct	2	Extreme
Number of stems	3	Few	3	Usually only 1 stem
Dwarfing—reduction in size of all parts of vine	4	Slight	1	Extreme
Delayed emergence	5	Distinct	5	Distinct
Blossom—conspicuous due to type of growth and late emergence	6	Conspicuous	11	Very conspicuous
Ruffling—waviness of margins of leaves	7	Slight	8	Distinct to extreme
Rugosity	8	Slight	19	Slight
Rolling—upward curving of the margins of leaf	9	Slight or absent	20	Absent
Wrinkling—irregular unevenness of leaf surface	10	Sometimes extreme when associated with chlorosis at emergence. Very slight or absent in large plants	9	Same as spindle tuber but more distinct in large plants
Chlorosis—yellowing of foliage	11	Occasionally extreme at emergence, but normal or slightly darker green in older plants	6	Same as spindle tuber but much darker green in older plants
Premature death	12	Slight	18	Distinct
Twisting of terminal leaflets	13	Occasional	10	Distinct
Spotting—necrotic areas of leaf [1]	14	Seldom	15	Occasional
Burning—necrotic areas at margin of leaf [1]	15	Seldom	16	Occasional
Curling—downward curving of leaf along midrib	16	Absent	7	Extreme
Rigidity	17	Absent	12	Distinct
Brittleness of stems and petioles	18	Absent	13	Distinct
Streaking—necrotic streaks on stems, petioles or leaf veins [1]	19	Absent	14	Occasional
Leaf dropping—premature death of lower leaves [1]	20	Absent	17	Occasional
TUBER SYMPTOMS				
Appearance of eyes at blossom end [2]	1	Distinct	1	Distinct
Increase in number of eyes	2	Distinct	3	Extreme
Increase in shallowness of eyes	3	Distinct	4	Extreme
Decrease in color or blotchy color	4	Distinct	5	Extreme
Cylindrical shape	5	Distinct	6	Distinct
Increase in length	6	Distinct	11	Distinct
Decrease in number	7	Distinct	7	Extreme
Protruding eye brows	8	Distinct	8	Distinct
Decrease in size	9	Slight	2	Extreme
Tenderness of skin	10	Slight	12	Distinct
Brittleness of flesh	11	Distinct	13	Distinct
Stolons thickened	12	Slight or absent	14	Distinct
Longitudinal cracks [1]	13	Occasional	9	Distinct
Increased number of lenticels	14	Slight	15	Distinct
Necrosis—areas on surface around lenticels [1]	15	Absent	17	Occasional
Necrosis—internal net necrosis [1]	16	Absent	18	Occasional
Irregular or bumpy surface—misshapen or tendency to knobs [1]	17	Absent	10	Distinct [1]
Abnormal development of sprouts to form tubers	18	Absent	16	Occasional

[1] Occur chiefly as current-season symptoms.
[2] See Plate 2 D.

toms were somewhat variable in their appearance under different conditions.

The description of the perpetuation symptoms[2] of these two diseases is given in Table 7 for the Bliss Triumph variety. The relative importance of each symptom as an aid in diagnosis is given and is based upon the stability and conspicuousness of the symptom under all the conditions tested. Many of the characters are quite variable under different environmental conditions, and thus the order of importance would of necessity vary under extreme conditions of environment.

Perpetuation symptoms in the vine.—It should be emphasized that the general appearance of the whole vine is of more importance than the appearance of each individual symptom. The five most important symptoms of both diseases are those which affect the appearance of the whole plant, and there is some question as to the relative importance of each of these five symptoms with spindle tuber. These first five symptoms are also less modified by environment than most of the other symptoms listed. As contrasted with spindle tuber, the extreme dwarfing and erect appearance of unmottled curly dwarf is quite characteristic (Plate 6). The rigidity, the darker green color, and extreme curling of unmottled curly dwarf are also of great value in distinguishing the diseases. The extreme decrease in the number of stems with unmottled curly dwarf and the decrease with spindle tuber as compared with a healthy plant are quite characteristic and are rather peculiar phenomena, inasmuch as the tubers and therefore the seed pieces have many more eyes than a healthy tuber. The waviness of the leaf margin, described as ruffling, is not listed by Schultz and Folsom (15) as a symptom of these diseases but it has been a persistent symptom in all plants examined by the author and is more extreme with unmottled curly dwarf. This ruffling, however, is not associated with severe wrinkling, such as is found with some of the mosaics. The yellowing of the foliage of young plants has been found to be quite variable and while healthy plants sometimes show a similar appearance, due to delayed emergence, it is much more common with infected plants. The twisting of terminal leaflets is very common with unmottled-curly-dwarf plants and occasionally occurs with spindle tuber. The necrotic symptoms of spotting, burning, streaking, and leaf dropping are quite variable and are more severe with unmottled curly dwarf than with spindle tuber. These symptoms also show great varietal modification and have always been more common and severe with Green Mountains than with Bliss Tri-

[2] "Perpetuation symptoms" refers to the symptoms occurring when infected tubers are planted as contrasted with "current season" symptoms, which develop the same year the plant becomes infected.

umphs. Folsom (3) lists spindle-tuber as being longer lived than healthy plants, while in Table 7 they are listed as shorter lived. This discrepancy is probably due to a different basis for determining the length of life, as pointed out on page 16. If the planting date is considered, spindle-tuber plants are longer lived than the healthy, while the reverse is true if the date of emergence is considered. As contrasted with spindle tuber, unmottled curly dwarf is distinctly characterized by premature death. It is evident from Table 7 that most of the symptoms are common to both diseases and that the difference lies, to a great extent, in the degree of severity.

Current-season symptoms in the vine.—The appearance of symptoms in the vines the same year that infection has occurred will of course vary with the time of infection.

When infection with spindle tuber occurs at planting time thru the seed piece, the symptoms will often develop early enough to be detected in the vines. The spindliness, uprightness, dwarfing, and decreased number of stems are not so noticeable, but the leaf characters, particularly the ruffling of the leaf margins and the acute angle of branching, are evident in the younger or upper portion of the vine. In general, however, the infected plants are very difficult to detect.

As contrasted with spindle tuber, the current-season symptoms of unmottled curly dwarf are very conspicuous. Inoculation of the seed piece at planting time often results in exactly the same symptoms as the perpetuation symptoms described above (Plate 7 A). In other instances such early infection does not show the extreme dwarfing but all other symptoms are present. With infection of the plant after emergence, usually the vine symptoms are very evident unless infection occurred late in the season. The current-season symptoms resulting from inoculation of a young plant, as contrasted with the perpetuation symptoms, are shown in Plate 6 B. The extreme dwarfing of the youngest foliage with the curling and twisting and the erect, rigid appearance is easily distinguished. The necrotic symptoms of spotting, burning, streaking, and leaf dropping often occur as current-season symptoms with unmottled curly dwarf, while spotting and burning sometimes occur with spindle tuber.

Perpetuation symptoms in the tuber.—The first nine symptoms listed in Table 7 are common to both diseases in the same order except for the decrease in size and increase in length combined with the longitudinal cracking which occurs with unmottled-curly-dwarf tubers. The four symptoms listed in the table as occurring with unmottled curly dwarf and as absent with spindle tuber are either extremely variable or occur only as current-season symptoms and are therefore

not as valuable for purposes of identification. With the above exceptions, all the other symptoms listed for spindle tuber occur usually in a more severe form with unmottled curly dwarf.

The first three symptoms listed in the table all relate to eye characters and have been found to be the most reliable symptoms in differentiating between healthy and infected tubers but are not of any great value in separating the two diseases. The number and position of the eyes, particularly at the bud end as shown in Plate 2 D, are always a reliable index of these diseases and these symptoms are less modified by environment than any of the others. The number of eyes on infected tubers is sometimes as high as 30 eyes on a tuber weighing only 75 to 100 grams. In one set of experiments the number of eyes was counted on infected and healthy tubers of equal weight, grown at the same time in the greenhouse, and it was found that the tubers from spindle-tuber plants averaged 45 to 50 per cent and those from unmottled-curly-dwarf 55 to 60 per cent more eyes than the healthy tubers.

The decrease in the color of Triumph potatoes is greatly influenced by environment. Nevertheless, this symptom was found to be one of the first to appear on infected tubers and is placed as of equal importance with the cylindrical shape. The cylindrical shape, which takes into account both the increased length and depth of the tuber, is more reliable than the increased length alone.

The increased length of infected tubers has been used by several investigators as a reliable index of spindle tuber. In Table 7 it is not considered as important as the above-mentioned characters with spindle tuber and is of even less importance with unmottled curly dwarf. Schultz and Folsom (15) measured the dimensions of different lots of tubers and found the ratio calculated for W/D (width/depth) to be more significant than the L/W (length/width). They state that "there is a high correlation between mechanically determined dimensions and diagnosis of the spindling-tuber disease from tuber symptoms." Werner (12) uses the W/L (width/length) expressed in percentage as an index of spindle tuber. He considers this more reliable than the W/D ratio. Werner considers, however, that an estimation of tuber type, "based on a consideration of the shape and all other tuber characters" and designated by an index number, is the most reliable method of stating the spindle tuber content of a lot of potatoes. He considers that this gives both the percentage of spindle tuber and the degree of severity of the disease. According to Schultz and Folsom (15) and the author's investigations, there is no change in the degree of severity of the disease

with succeeding generations after the first year except as the symptoms are temporarily modified by environment. Data based upon tuber type would therefore be less accurate than a simple statement of the percentage of infected tubers. The shape of both healthy and infected tubers has been shown to be greatly modified by environmental conditions. Therefore, any ratio based upon the dimensions of the tuber is subject to considerable error and the author has found it impossible to determine correctly the percentage of infected tubers by using tuber measurements.

In 1924 tuber measurements were made of one tuber from each hill of an experimental plot, and plants were grown from these tubers in the greenhouse and in the field the following year. The tubers selected for measuring and indexing were those which were the most elongated and appeared the most like spindle tuber even tho no vine symptoms had been present in the field. In case the vines showed distinct spindle-tuber symptoms, those tubers which had the most severe symptoms and were the most elongated were selected. All of the tubers were of No. 1 size and approximately the same weight. Tubers which produced healthy plants the following year had an average L/W ratio for 237 tubers of 1.152. Tubers from plants which appeared healthy but were infected late in the season and produced spindle-tuber plants the following year had an average L/W ratio of 1.163. The tubers from typical spindle-tuber plants had an average L W ratio of 1.250. The length in proportion to the width is greater for the spindle-tuber potatoes but the difference is not large enough to serve as a means of separating the healthy from the infected. This was clearly evident from the fact that 88 per cent of the healthy tubers were longer than wide, altho the Triumph is considered to be a round variety. Furthermore, 25 per cent of the healthy tubers had a L/W ratio greater than that of the spindle-tuber potatoes showing the most severe symptoms, and grown in the same experimental plot.

In addition to these facts, it is also true that in the case of the Triumph variety the tuber becomes longer in proportion to its width as it increases in size and for this reason the largest tubers will always have a greater L W ratio. It seems evident, therefore, that any ratio based upon tuber measurements can be used in only a relative manner as an index of the spindle-tuber content of one lot of seed in comparison with another lot grown under similar conditions and where the tubers are approximately the same size.

The decrease in the size of tubers is much more evident with unmottled curly dwarf than with spindle tuber. This can be shown by one example which occurred in an experimental plot where 25 unmottled-curly-dwarf hills were

planted in a row and the tubers produced averaged only 33 grams each, while 25 spindle-tuber hills in the same row averaged 84 grams per tuber. The number of tubers per hill was 6.6 for the spindle-tuber hills and 2.2 for the unmottled curly dwarf. This severe reduction in the yield of unmottled-curly-dwarf hills occurred under ideal conditions for growth in an irrigated plot where healthy hills cut back to a single stalk yielded 1,096 grams per hill.

This experiment, which had been conducted for another purpose, also proved to be a good example of the effect of environmental factors on the symptoms of these diseases, the effect being similar to that which occurred in the experiments under controlled conditions. In a season of fairly low temperatures and with abundant moisture supplied by irrigation, the spindle-tuber plants could be detected only during their early growth. After one month it was practically impossible to pick out these 25 hills from adjacent healthy rows. When the tubers were dug they were found to have all the typical symptoms and every tuber could have been easily picked out of a bin of healthy potatoes. The tubers were of good size, however, and the set was not greatly reduced, the hills averaging over 500 grams per hill. On the other hand, the unmottled-curly-dwarf hills were easily identified at all times during the growing season and the entire 25 hills yielded less than 2 kilograms without a single No. 1 size potato.

Longitudinal cracks are commonly present with unmottled curly dwarf, particularly as a current-season symptom, in which case they occur on the irregular, misshapen tubers, often without any other evidence of the disease. Tubers of this type are pictured in Plate 5 A-2, 3, resulting from inoculation in late July of plants from late May planting. Cracking also occurs as a perpetuation symptom but it is not so consistent. It is customary to find that about 50 per cent of the hills planted with infected seed contain tubers with cracks, but not all the tubers in a hill show cracking. The absence of cracks does not mean that the disease is not unmottled curly dwarf, but the presence of cracking is strong evidence of the disease, as spindle tuber seldom causes cracking.

The tubers affected with either disease often show a distinct brittleness of the flesh. Cutting causes a sharp, crackling noise and the tubers are easily split. The number of lenticels on infected tubers is usually much greater and more evident with unmottled curly dwarf than with spindle tuber. Infected seed pieces, with both diseases, often remain sound and firm after the healthy seed pieces under the same conditions are entirely used up. This is characteristic and seems to be correlated with the slower, weaker type of growth of infected plants from such seed pieces.

The necrotic areas occurring on the surface of tubers and the internal necrosis listed in Table 7 have been observed only with unmottled curly dwarf, and this necrosis has not occurred consistently. In 1927 necrotic areas were noted on the surface of about 30 per cent of the tubers produced from seed infected with unmottled curly dwarf and on 80 per cent of the tubers from inoculated seed pieces. These necrotic areas appeared to start around the lenticels and the spots often enlarged and met to cover half the surface of the tuber. It was at first thought that this might be due to an epidemic of early blight that occurred in neighboring fields that year. The experimental plot, however, was sprayed every ten days and blight did not become severe. Furthermore, the healthy tubers in adjoining rows were not affected. Cultures from these necrotic areas proved to be sterile. Further examination of all tubers produced in the plot made it evident that this symptom was associated with unmottled curly dwarf. Only occasional tubers have been found since that year and the occurrence of a similar symptom has been noted in the soil moisture and temperature experiments.

It was also noted in the same experiment that some of the unmottled-curly-dwarf tubers were affected with an internal necrosis not directly connected with the surface discoloration. This appeared as a light browning of the tissue in the vascular region (Plate 5 B-2, 3) occurring either as streaks or flecks and in some cases most of the tissue of the tuber except the center was deeply discolored. This internal necrosis also occurred with tubers from plants inoculated in midsummer. Such tubers did not show any surface necrosis and the internal necrosis in some cases appeared somewhat similar to Fusarium wilt and in others more like the net necrosis of leaf roll. Cultures of this tissue also proved to be sterile. Most of these tubers were from tuber unit plantings with one or more healthy checks in each unit. None of these checks produced tubers similarly affected and the internal necrosis was clearly correlated with the unmottled-curly-dwarf inoculation.

It might also be noted in connection with the above symptoms that in every instance plants grown from such tubers produced typical unmottled-curly-dwarf plants and tubers which only occasionally were affected with similar necrotic symptoms. Neither leaf roll, streak, nor wilt was found in any of the plants and other plants of the same variety affected with these diseases did not show symptoms similar to these described. In 1928 a small number of tubers with internal necrosis were found, following current-season infection, but the surface necrosis did not occur.

Current-season symptoms in the tubers.—Occasionally infected tubers appear to be perfectly normal even when the

vine was infected early in the season. On the other hand the tubers will sometimes show distinct symptoms when the vines appear healthy. In general the eye characters are the first reliable symptoms, altho the decreased color and increased length are sometimes evident.

The current-season tuber symptoms of unmottled curly dwarf are quite distinct from those of spindle tuber. If infection occurs early in the season, the tubers are usually about the same as described for the perpetuation symptoms; but with infection occurring at about the time the tubers are forming, the symptoms are quite different. The longitudinal cracks are more pronounced with unmottled curly dwarf and the tubers, while large and well colored, are often misshapen with abnormal eyes (Plate 5 A-2, 3). The cracking and the bumpy, irregular shape are the most characteristic symptoms, and occur with tubers which, if infected at the same time with spindle tuber instead of unmottled curly dwarf, would not be distinguishable from healthy tubers. The necrotic symptoms listed in Table 7 sometimes occur as current-season symptoms in such tubers.

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PLATE 1

A—(1) Unmottled-curly-dwarf and (2) spindle-tuber plants grown in the greenhouse from infected seed tubers. Early fall planting.

B—(1) Unmottled-curly-dwarf, (2) spindle-tuber, and (3) healthy plants grown from seed tubers harvested at same time as those of A, but planted later in the greenhouse.

C—Unmottled-curly-dwarf plants from different portions of the same tuber planted (1) December 13, (2) January 10, (3) February 12. All photographed on the same day. (See page 11.)

PLATE I

PLATE 2

Seed tubers (A, healthy; B, spindle tuber; and C, unmottled curly dwarf) used for the soil moisture and temperature experiments.

D—Showing the eye characters at the bud end of (1) a healthy tuber as compared with (2) one infected with spindle tuber.

PLATE 2
A
B
C
D-1
D-2

PLATE 3

A—Unmottled curly dwarf plants grown at (1) 1⅓, (2) 1, and (3) ⅔ times the soil moisture equivalent.

B—Unmottled curly dwarf; C, spindle tuber; and D, healthy tubers grown at (1) 1⅓, (2) 1, and (3) ⅔ times the soil moisture equivalent.

PLATE 3

PLATE 4

A—Healthy; and B, unmottled-curly-dwarf tubers; grown at (1) 30°, (2) 25°, (3) 20°, and (4) 15° C. soil temperature.

C—Unmottled-curly-dwarf plants in early stages of growth at (1) 30°, (2) 25°, (3) 20°, and (4) 15° C. soil temperature.

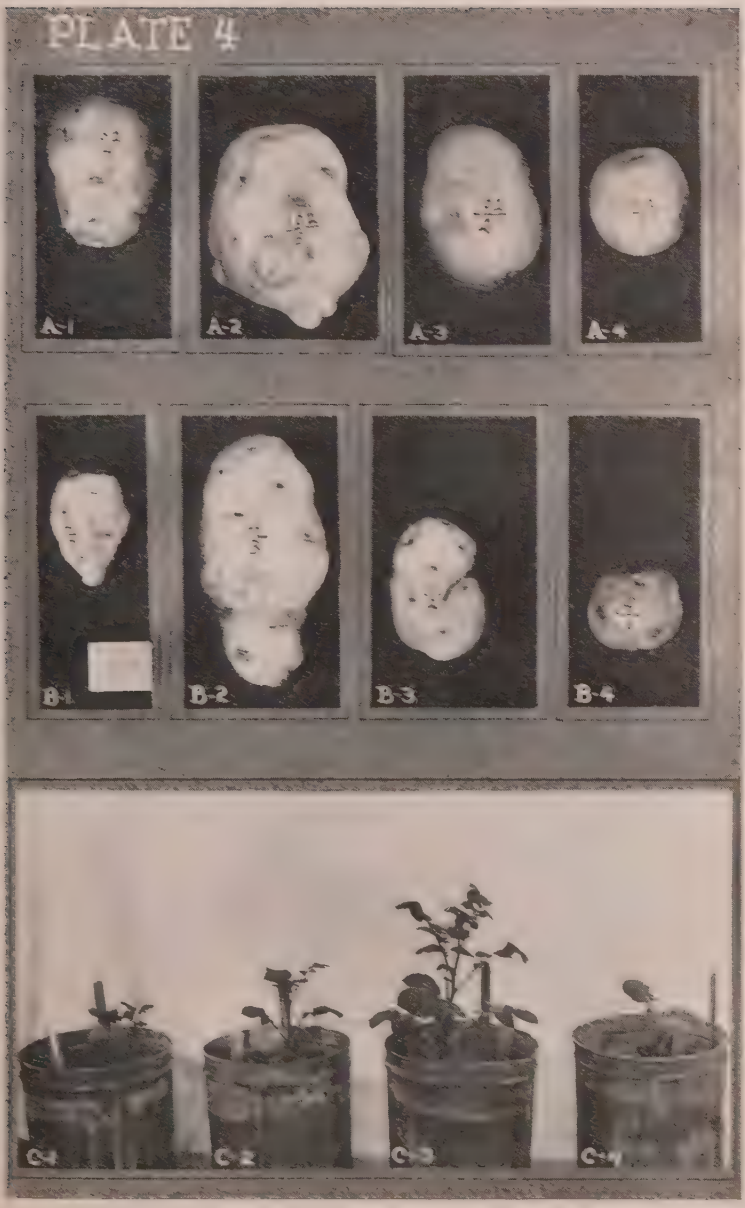


PLATE 4
A-1
A-2
A-3
A-4
B-1
B-2
B-3
B-4
C-1
C-2
C-3
C-4

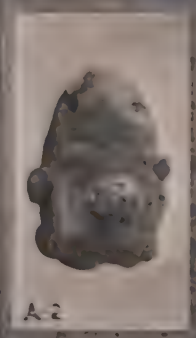
Plate 5

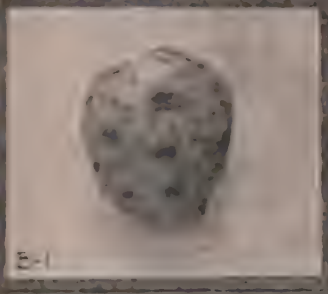
A—(1) Type of sprout tubers produced by unmottled-curly-dwarf seed in the soil moisture and temperature experiments (see pages 15 and 20). (2) (3) Type of misshapen tubers showing current-season symptoms resulting from juice inoculation of foliage with unmottled curly dwarf.

B—(1) Type of surface necrosis centered around the lenticels of unmottled-curly-dwarf tubers in the soil moisture experiment (see pp. 17 and 37). (2) (3) Internal necrosis sometimes occurring with unmottled curly dwarf.

C—Comparison of sprout development showing lack of apical dominance with spindle tuber. Left, healthy; center and right, spindle tuber.

PLATE 5





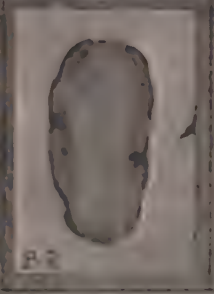


Plate 6

A—Young plants in field showing perpetuation symptoms of (2) spindle tuber and (3) unmottled curly dwarf as compared with (1) healthy check.

B—Current-season symptoms resulting from juice inoculation at emergence with (2) spindle tuber and (3) unmottled curly dwarf as compared with (1) healthy check.

Note: The light spots on the leaves in A-1 and B-1 are due to spray.

PLATE 6

Plate 7

A—Current-season symptoms resulting from inoculation of the seed piece with unmottled curly dwarf. (1) Healthy check, (2) (3) inoculated, (4) unmottled curly dwarf from seed tuber used as the source of inoculum.

B—Detail of type of branching occurring in the field: (1) normal, (2) spindle tuber, and (3) unmottled curly dwarf.

Note: The light spots on the leaves in B-1 and 2 are due to spray.

PLATE 7
A-2
B-2